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Artículo Original

DISTRIBUTION IN VENEZUELA OF THE BATS *Promops centralis* THOMAS 1915 AND *P. nasutus* (SPIX 1823) (CHIROPTERA: MOLOSSIDAE): INSIGHTS FROM MUSEUM SPECIMENS AND ACOUSTIC RECORDS

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ABSTRACT. The distributions in Venezuela of the bats *Promops centralis* and *P. nasutus* are updated, based on information from museum specimens and acoustic records. *P. centralis* has the most extensive geographic range within the country, with records from 34 locations and nine bioregions, while *P. nasutus* has a more restricted range with 17 locations and seven bioregions. This new data expands the previously known distribution of these species, with the first records of *P. nasutus* in the northern coastal region. The vocal signatures are visually different and readily identifiable from those of other molossids and consistent with the patterns previously described in the scientific literature. The characteristic frequency of the dominant harmonic was the most useful acoustic parameter to identify echolocation calls. Both species are found mostly in open spaces associated with forest vegetation and water bodies, with more records of *P. centralis* in disturbed environments. This study highlights the importance of acoustic sampling for studying aerial insectivorous bats, providing a better understanding of their distributions, relative abundances, and ecological preferences than capture methods alone. Some aspects with implications for conservation are discussed.

RESUMEN. DISTRIBUCIÓN EN VENEZUELA DE LOS MURCIÉLAGOS *Promops centralis* THOMAS 1915 Y *P. nasutus* (SPIX 1823) (CHIROPTERA: MOLOSSIDAE): PERSPECTIVAS A PARTIR DE ESPECÍMENES DE MUSEOS Y REGISTROS ACÚSTICOS. Se actualizan las distribuciones en Venezuela de los murciélagos *Promops centralis* y *P. nasutus*, sobre la base de la información obtenida de especímenes de museo y registros acústicos. *P. centralis* muestra el rango geográfico más amplio en el país, con registros en 34 localidades y nueve bioregiones, mientras que *P. nasutus* tiene un rango más restringido con 17 localidades y siete bioregiones. Los nuevos datos amplían las distribuciones previamente conocidas para estas especies, con los primeros hallazgos de *P. nasutus* en la región norte costera. Sus señales vocales son visualmente diferentes y fácilmente identificables respecto de las de otros molósidos y, además, son consistentes con los patrones descritos previamente en la literatura científica. La frecuencia característica de la harmónica dominante fue el parámetro acústico de mayor utilidad para identificar las llamadas de ecolocación. Ambas especies son halladas frecuentemente en espacios abiertos asociados con vegetación boscosa y cuerpos de agua, con un mayor número de registros de *P. centralis* en ambientes perturbados. Este estudio resalta la importancia de los muestreos acústicos para el estudio de murciélagos insectívoros aéreos y aporta un mejor entendimiento de sus distribuciones, abundancias relativas y preferencias ecológicas con relación a los métodos basados exclusivamente en capturas. Se discuten algunos aspectos con implicancias en materia de conservación.

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Palabras clave: Insectívoros aéreos, Patrones geográficos, Ecolocación, Molósidos, Región Neotropical, Sur América.

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INTRODUCTION

Three aerial insectivorous species are currently recognized among the bats of the genus *Promops* Gervais 1856 (Molossidae), which occur over a wide range of ecological conditions throughout the Neotropics (Eger 2008; Froidevaux et al. 2020; Hintze et al. 2020): *Promops centralis* Thomas 1915, *P. davisoni* Thomas 1921, and *P. nasutus* (Spix 1823). Of the three, *P. centralis* has the widest geographic distribution, ranging from Sonora in northern Mexico, through Central America, Trinidad and Tobago, northern South America, and the Amazon basin, to eastern and southern Brazil, Paraguay, and central Argentina, with an altitudinal range from sea level to 2400 m (Genoways & Williams 1979; Jones et al. 1988; Soriano et al. 2005; Barnett et al. 2006; Eger 2008; González-Terrazas et al. 2016; Fernández de Córdova et al. 2017; Hintze et al. 2020; Montani et al. 2020). The other two species are known only from South America, where *P. davisoni* appears to be restricted to lowlands and midlands of the western slope of the Andes, including the coastal strip of Ecuador, Peru, and northernmost Chile (Gregorin & Chiquito 2010; Flores et al. 2015; Ossa et al. 2018), while *P. nasutus* has a wider distribution ranging from sea level to 2560 m, with records from Colombia, Trinidad and Tobago, part of southern Venezuela, and the Guiana Shield, extending to eastern and southern Brazil, southern Bolivia, Paraguay, and central Argentina (Eger 2008; Gregorin & Chiquito 2010; Rufray 2015; Paqui et al. 2016; Montani et al. 2020; Sales & da Rocha 2024). There are no records of *P. nasutus* in the Amazon basin or central Brazil.

Members of the genus *Promops* are represented by relatively few specimens in zoological collections, and they are rarely documented in field surveys (Froidevaux et al. 2020). This is similar to other aerial insectivorous bats that forage in open areas and are high-flying (e.g., *Diclidurus* spp., *Nyctinomops* spp., and *Eumops* spp.), limiting their collection or detection based on capture methods (Ochoa et al. 2000; Schnitzler & Kalko 2001; MacSwiney-G et al. 2008; Jung et al. 2014; Yoh 2018; Miller et al. 2024). As a result, *Promops* species either appear absent or, if present, only at an apparent very low relative abundance throughout their geographic ranges (e.g., Handley 1976; Hintze et al. 2020; Montani et al. 2020). This has been misleading, resulting in poorly understood importance of the genus in mammal communities and ecosystems.

The first record of *Promops* in Venezuela was reported by Tate (1947), based on a single specimen of *P. centralis* collected at Rancho Grande, Henri Pittier National Park (Aragua State). Twenty-four years later, Ojasti & Linares (1971) apparently missed this reference and erroneously mentioned that a specimen found in Caracas was the first record of the genus for Venezuela and South America, providing additional notes on the taxonomic distinction of some congeneric forms. Subsequently and as part of a mammal survey conducted by the Smithsonian Venezuelan Project (Handley 1976), a third specimen of *P. centralis* was recorded in Venezuela, in addition to the first record of *P. nasutus*; both reports correspond to specimens collected in the southern region of the country (Bolivar and Amazonas States). During the following years, two additional records of *P. centralis* were published (Ochoa & Ibañez 1985) and three years later Linares (1998) presented a compilation of the available information on the distributions of the species of *Promops* known in the Venezuelan territory. This author described a geographical range for *P. centralis* defined by four localities in the Cordillera de la Costa, the Eastern llanos, and the northern extreme of the Guayana region, while *P. nasutus* was reported to be restricted to the south of the Orinoco River. Until now, the presence in Venezuela of only these two congeneric species is confirmed in the most recent mammal checklists for the country (Sánchez & Lew 2012; Boher et al. 2023).

Over the last 34 years, several studies supported primarily by Venezuelan institutions responsible for

zoological collections have provided additional data on the biology and natural history of species of *Promops* (Soriano et al. 2005; Ochoa et al. 2000, 2005, 2009; Jung et al. 2014). Most of these contributions included acoustic sampling methods, focusing on the detection and analysis of the acoustic signals of insectivore bats whose feeding strategies are based on the capture of prey in the air. This enhanced the understanding of the geographic ranges and ecological preferences of the genus *Promops* and other taxa throughout the country, highlighting their importance in different ecosystems.

Call shapes of the vocal signatures of *Promops* are visually distinct and readily distinguishable from other genera in the family Molossidae (Jung et al. 2014; Ossa et al. 2018; Hintze et al. 2020; Sales & da Rocha 2024) and are not likely to be confused with other species. They have distinctive ascending Frequency Modulation (FM-frequencies vary according to the amplitude of the modulating signal) pulses, often with interspersed descending FM pulses in a range from 5 kHz to 10 kHz above the maximum value of ascending pulses (**Fig**. 1A). Commuting calls are also unique in *Promops* and consist of a relatively long Constant Frequency (CF) component (**Fig**. 1B), followed by a shorter ascending FM component at the same frequency range as search phase calls (Jung & Kalko 2011; Barataud et al. 2013; Jung et al. 2014; González-Terrazas et al. 2016; Arias-Aguilar et al. 2018; Froidevaux et al. 2020; Hintze et al. 2020).

To contribute to the knowledge of Neotropical bats whose biology remains poorly documented, we update the distributions of *P. centralis* and *P. nasutus* in Venezuela, with significant expansions of their previously known geographic ranges. We also highlight the need to include acoustic sampling for a better evaluation of the occurrence of aerial insectivorous species that can be underestimated when only capture methods are used (MacSwiney-G et al. 2008; Arias-Aguilar et al. 2018), in addition to providing complementary data on the ecological preferences of the genus *Promops* and its importance as a community component in a wide range of ecosystems.

MATERIALS AND METHODS

The information used in this study is based on historical records supported by museum specimens and the results of new field surveys combining capture methods (mist nets and harp traps) and acoustic sampling. In the first case, we consulted published literature and collection databases, including VerNet (www.vertnet.org), SpeciesLink (www.splink.cria.org.br), and Global Biodiversity Information Facilities (www.gbif.org). Additionally, one of us (JOG) reviewed the reference data of voucher specimens deposited in the following institutions: VENEZUELA: Colección de Vertebrados de la Universidad de Los Andes (CVULA, Mérida), Museo de la Estación Biológica de Rancho Grande (EBRG, Aragua), Museo de Biología de la Universidad Central de Venezuela (MBUCV, Distrito Capital), and Museo de Historia Natural La Salle (MHNLS, Distrito Capital); USA: American Museum of Natural History (AMNH, New York) and Museum of Texas Tech University (TTU, Lubbock).

Field surveys were conducted throughout the country from 1999 to 2022, some as components of larger projects focused on assessing mammal communities across different geographical regions and ecosystems. Survey dates coincided with rainy and dry seasons and periods with low lunar illumination. Sampling sites were selected in areas where only a single species of *Promops* was expected (*P. centralis*) or where the sympatry of the two congeneric forms recorded in the country was assumed based on historical information. At each survey site, we set mist nets (6-12 m in length) at sites associated with forest vegetation or water bodies (rivers and lagoons), with a vertical coverage of 0.2-3 m, although at some sites stacked nets increased the height to six meters. Field evaluations also included passive and/or active acoustic sampling in most sites, simultaneously with the captures of voucher specimens (Jung et al. 2014; González-Terrazas et al. 2016); this procedure followed the protocols suggested for the acoustic recording of aerial insectivore bats (Ochoa et al. 2000).

The early passive and active acoustic recordings were in real time, with Anabat II detectors linked to laptop computers using a Zero-crossings Analysis Interface Module. More recently, an Anabat Express (Titley Scientific) was used for active and passive detections. Passive detectors were set at fixed sites with omnidirectional microphones directed towards open areas associated with forest vegetation, water bodies, urban environments, or a combination of at least two habitat types to document species occurrence in structurally different ecological conditions. Active acoustic sampling included transects from boats along rivers and lagoons using a hand-held detector in areas surrounded by humid forests as the dominant vegetation. Acoustic files were recorded and saved in zero crossings format (ZC).

Diagnostic call shapes and acoustic parameters were analyzed using AnalookW (ver. 4.6. m; Corben 2022a). The dominant harmonic's characteristic frequency (Fc) was the main parameter for species recognition because it is readily measured and compared regardless of the mode of recording (i.e., ZC or full spectrum). It is important to highlight that in some publications, the Fc and the frequency with the maximum energy (FME) or concentration of energy (COE) are used interchangeably, but they are not the same and may differ considerably; therefore, they may not be directly comparable (Miller & Corben 2022). We also used the Characteristic Slope (Sc) or the slope of the body of the call, as it is an important feature for call evaluation and a key way in which different species with similar Fc values can differ (Corben 2022b). Other call frequency parameters measured in kilohertz (kHz) were minimum frequency (Fmin), maximum frequency (Fmax), and average frequency (Fmean), in addition to the following time parameters measured in milliseconds (ms): duration of each pulse (Dur) and the inter-pulse interval or time

Fig. 1. A. Typical *Promops* search phase call sequence, with both the increasing FM pulses immediately followed by the higher frequency decreasing FM pulses. **B.** Typical and unmistakable *Promops* commuting calls with a long CF component and a trailing ascending FM component. The Zero-crossings display has a logarithmic frequency scale, and the time between pulses is condensed to show diagnostic call sequences.

between calls (TBC). Five derived values included the Fc of both the fundamental (FcH1) and third harmonic (FcH3), the proportion of maximum frequency to the characteristic frequency (PMC), the bandwidth (Fmax-Fmin), and the pulse repetition rate per second (PRR).

Reference calls used for acoustic identifications of recordings during this study included 1400 verified acoustic records of *P. centralis* from Belize (recorded by BWM between 1995 and 2012) and verified calls from the first recording of *P. nasutus* from Bolivia in 2005 (Siles, pers. comm). The R programming language summarized descriptive statistics for each species' vocal signatures (R Core Team 2022). These summaries include the number of pulses measured (*N*) for each parameter, the minimum and maximum values, the mean, the standard deviation, and the 10^{th}, 25^{th}, 75^{th}, and 90^{th} percentiles. The percentiles provide an indication of the variation and range of call parameters beyond the mean and standard deviation, with 25% to 75% showing where 50% of the calling values occur, while 10% to 90% shows where 80% of the values occur.

The collections of voucher specimens conducted during this study were under permits issued by the Venezuelan government within the framework of two projects: 1) La Diversidad Biológica de la Cuenca del Río Caura: Caracterización, Vocación y Prioridades de Conservación (FONACIT 98003392), supported by the Fondo Nacional de Ciencia y Tecnología; and 2) Conservación y Uso Sostenible de la Diversidad Biológica en la Reserva de Biósfera Delta del Orinoco (MARN and PNUD-VEN/99/G31), supported by the Ministerio del Ambiente y de los Recursos Naturales in association with PNUD. All collecting and live animal handling followed accepted protocols (Jung et al. 2014; Sikes & The Animal Care and Use Committee of the American Society of Mammalogists 2016). Voucher specimens were deposited in the mammal collection of the Museo de la Estación Biológica de Rancho Grande (EBRG), Maracay, Aragua State (Appendix 1), which is administrated by the Ministerio del Poder Popular para el Ecosocialismo.

The coordinates of each historical record were reviewed and, when necessary, georeferenced and adjusted to reflect location accuracy within 100 m. Broad habitat associations were extracted for each species location using ArcGIS Desktop (ESRI 2022) and the Xtools Pro Identity tool (XTools 2022), where location points are related to features for all overlapping spatial layers. As with another recent study of aerial insectivorous bats (Miller et al. 2024), we used spatial layers that included updated bioregions, states, vegetation classes (Huber 1997; Huber & Oliveira-Miranda 2010), water bodies, rivers, and a generalized grid of elevations (1 km^2).

The Venezuelan bioregions were updated from the previous version of MARN (2001) using ArcGIS Desktop (ESRI 2022). To derive habitat associations and the distribution map, we used the updated bioregions of Miller et al. (2024) that divided the former Llanos into three distinct areas, as Huber (1997) and Sánchez & Bisbal (2003) proposed. Additionally, the region south of the Orinoco River, frequently called in previous literature as the Venezuelan Guayana, was subdivided into three distinct areas, according to Madi et al. (2011). Based on these criteria, the following bioregional units were considered (**Fig.** 2): Islands (ISL), Continental Coastal Strip (CCS), Maracaibo Lake Depression (MLD), Lara-Falcón-Yaracuy Hill System (LHS), Central Coast Mountain Range (CCR), Eastern Coast Mountain Range (ECR), Andes of Perijá (AOP), Andes of Mérida (AOM), Low Llanos (LOL), Central Western Llanos (CWL), Eastern Llanos (ELL), Deltaic Plains (DEP), Piedmont, Plains and Low Hills of Guyana (PPH), Floodplains of the High Middle Orinoco (FPO), and Mountainous Tepuyan System of the Guiana Massif (MTG).

In addition to the association of each species with the altitudinal gradient and the bioregional units described

above, we developed a matrix based on a general description of the landscape surrounding each recording place within a circular area defined by a radius of five km around the sampling point (Miller et al. 2024). For this, we selected the following attributes: 1) presence of forest vegetation and extent of its cover (continuous in all the evaluated area vs. discontinuous in association with a non-forest matrix); 2) presence of freshwater bodies in open spaces accessible to molossid bats (lagoons or rivers); 3) occurrence of extensive anthropogenic activities (e.g., urban development, agriculture, opencast mining, or industrial logging); and 4) presence of aerial strata devoid of tree cover above and around each sampling point. These were derived from field notes and Google Earth images (Google Earth 2022) corresponding with or approximate to survey dates. Each attribute was evaluated independently within the set of locations recorded per species, obtaining a frequency of occurrence to indicate the predominant landscape conditions in the evaluated sites.

RESULTS

Acoustic identifications

Vocal signatures of *P. centralis* and *P. nasutus* recorded during this study matched the call parameters previously described for each species. **Table** 1 and **Table** 2 present diagnostic parameters and derived values for both species, including those corresponding to records from Venezuela. The Fc of the dominant harmonic was found to be the most robust parameter for acoustically differentiating *P. centralis* and *P. nasutus* (**Fig**. 3), as the ranges of the Fc and other parameters do not overlap (see **Table** 1 and **Table** 2).

Diagnostic calls used for the identification of both taxa were distinct FM pulses with increasing frequencies and decreasing FM pulses in higher ranges (see **Fig**. 1A). Both higher and lower frequency pulses are usually emitted in an alternating pattern in the same sequence during search or approach phase calls, and their shapes are also distinct from other species. Depending on what the bat was doing, occasionally only the increasing FM lower frequency pulses are recorded without the upper decreasing pulses. Such pulses are diagnostic for species identification even when the upper and decreasing pulses are undetected.

Commuting calls (see **Fig**. 1B) were an important complement confirming the presence of *Promops*. They were occasionally recorded and distinct as constant frequency (CF) pulses of relatively long duration (Dur) at the initial portion (see **Fig**. 1B), showing a variation of the pulse duration ranging from 25 ms to 90 ms. The terminal part of such pulses corresponds to the increasing FM component seen in search phase calls. Such commuting calls are distinct, diagnostic, and readily identified as *Promops*, with different frequency ranges for each species. Such call sequences were more frequently recorded for *P. centralis* and usually were interspersed with diagnostic search phase calls. When detectors are set to translate ultrasounds to a human audible range, commuting calls produce a relatively low and very long sound. Additional sequences recorded include feeding buzz or terminal phase calls as individuals approach or capture their prey. Such calls have very short-duration broad-band "buzz" pulses that may either span the frequency range of both upper decreasing and lower increasing FM pulses or occasionally drop well below the lower increasing pulses (**Fig**. 4).

Distribution status and ecosystem affinities

We recorded species of *Promops* at 48 locations and nine of the 15 bioregions (Appendix 1, **Fig**. 2). Voucher specimens documented 58.3% of the records (28 locations), and the remaining records were based on acoustic samplings. Among all the locations recorded, only 18.7% had both specimen and acoustic data.

Of the two species, *P. centralis* has the widest distribution in Venezuela (see **Fig**. 2A, Appendix 1), with records from 34 locations corresponding to nine bioregions and an altitudinal range between 0 and 2000 m. Conversely, *P. nasutus* was recorded at 17 locations (see **Fig**. 2B, Appendix 1) and seven bioregions, suggesting a more restricted geographic range at altitudes from sea level to 1.080 m.

All sampling points with either *P. centralis* or *P. nasutus* records were characterized by the proximity to forests with different patterns of spatial distribution. In some cases, forests were continuous with extensive coverage, while in other opposite situations, these ecosystems corresponded to interconnected or isolated fragments whose spatial dispositions, after intensive modifications linked to anthropogenic impacts, were restricted to the banks of the main drainage lines, in association with a broader matrix of secondary non-forested vegetation (mainly herbaceous).

P. centralis had the highest proportion of records in areas with a reduction of the original forest coverage (67.6% vs. 35.3% in *P. nasutus*), as well as in areas extensively disturbed (70.6% vs. 47.1% in *P. nasutus*). The main anthropogenic impacts on the ecological conditions around sampling points are derived from agriculture (including livestock), mining, wood extraction, and urban development.

Table 1

Values of selected call parameters of *Promops centralis* from Venezuela, with Fc being the H2 or dominant harmonic. Derived variables are denoted with an asterisk. N represents the number of pulses measured. Values reflect the minimum, maximum, mean, standard deviation, 10^{th}, 25^{th}, 75^{th}, 90^{th} percentiles, and median values of the total call pulses.

Variable	N	Min	Max	Mean	Std. Dev.	10%	25%	Median	75%	90%
Dur	2355	5.0	139.2	15.3	12.3	6.3	8.4	13.2	16.9	24.3
TBC	1763	6.0	257.9	101.0	87.3	9.6	18.5	81.8	186.4	234.2
Fmin	2355	23.0	28.8	25.2	1.4	23.3	24.1	25.1	26.2	27.4
Fmax	2355	23.3	29.0	26.9	1.1	25.6	26.1	26.9	27.6	28.5
Fmean	2355	23.1	28.9	26.2	1.2	24.8	25.5	26.2	27.0	27.9
FcH1*	2355	11.5	14.5	13.4	0.6	12.7	13.0	13.4	13.7	14.1
Fc	2355	23.0	29.0	26.7	1.1	25.4	26.0	26.8	27.5	28.2
FcH3*	2355	34.5	43.5	40.1	1.7	38.0	39.0	40.1	41.2	42.3
S1	2355	-431.8	383.6	-15.0	39.8	-46.5	-32.0	-18.0	5.4	23.9
Sc	2355	-14.9	7.9	-4.8	4.0	-9.5	-7.3	-5.2	-1.9	0.0
Pmc*	2355	0.0	13.9	0.7	1.6	0.0	0.0	0.0	0.7	2.0
BW*	2355	0.1	5.2	1.6	0.9	0.5	0.9	1.6	2.2	2.8
PRR*	1763	3.9	166.7	35.5	40.3	4.3	5.4	12.2	54.1	104.4

Table 2

Values of selected call parameters of *Promops nasutus* from Venezuela, with Fc being the H2 or dominant harmonic. Derived variables are denoted with an asterisk. N represents the number of pulses measured. Values reflect the minimum, maximum, mean, standard deviation, 10^{th}, 25^{th}, 75^{th}, 90^{th} percentiles, and median values of the total call pulses.

Variable	N	Min	Max	Mean	Std. Dev.	10%	25%	Median	75%	90%
Dur	1033	4.0	24.0	11.3	3.8	6.1	8.5	11.4	13.6	15.8
TBC	692	110.1	378.4	198.8	77.3	118.3	127.4	196.8	244.9	326.6
Fmin	1033	31.6	34.9	33.2	0.7	32.1	32.7	33.2	33.7	34.1
Fmax	1033	33.4	39.1	35.6	0.8	34.6	35.2	35.6	36.2	36.5
Fmean	1033	32.9	36.0	34.9	0.7	33.9	34.4	34.9	35.4	35.7
FcH1*	1033	16.6	18.6	17.8	0.4	17.2	17.5	17.8	18.1	18.2
Fc	1033	33.2	37.2	35.5	0.7	34.5	35.0	35.6	36.1	36.5
FcH3*	1033	49.8	55.8	53.3	1.1	51.7	52.5	53.4	54.2	54.7
S1	1033	-442.8	732.5	-30.8	59.2	-52.5	-38.2	-26.4	-19.7	-12.6
Sc	1033	-15.0	7.2	-6.7	2.7	-10.3	-8.1	-6.3	-5.0	-3.9
Pmc*	1033	0.0	13.9	0.2	0.8	0.0	0.0	0.0	0.2	0.7
BW*	1033	0.4	6.9	2.4	0.8	1.5	2.0	2.4	2.9	3.5
PRR*	692	2.6	9.1	5.8	2.1	3.1	4.1	5.1	7.8	8.5

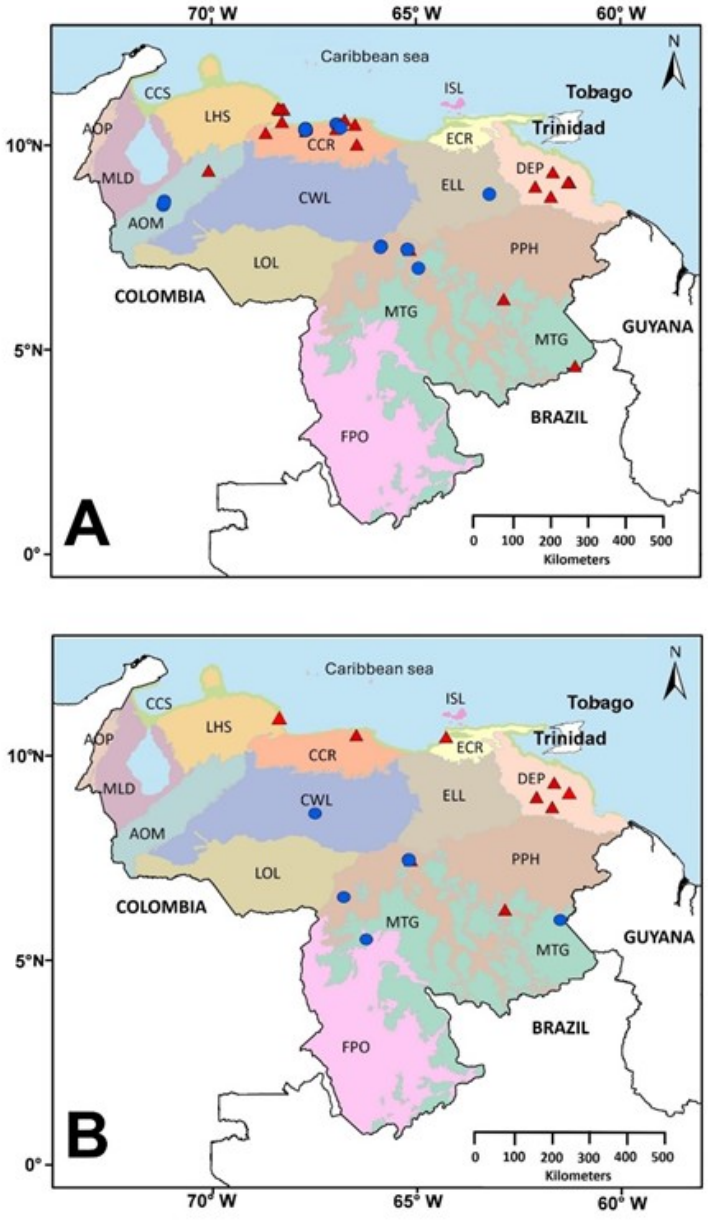

Fig. 2. Known distribution of *Promops centralis* (A) and *P. nasutus* (B) in Venezuela. Data obtained from acoustic records (triangles) and other sources of information (circles). The geographic units correspond to the bioregions as defined in Materials and Methods.

For both species, more than 97% of the sampling points coincided with open space devoid of tree cover, and a high proportion corresponds to areas characterized by the presence of open water bodies (82.4%-100%).

DISCUSSION

Field studies of bats combining sampling methods that include capture, collection of voucher specimens, and acoustic sampling are particularly important for high-flying aerial insectivores that oth-

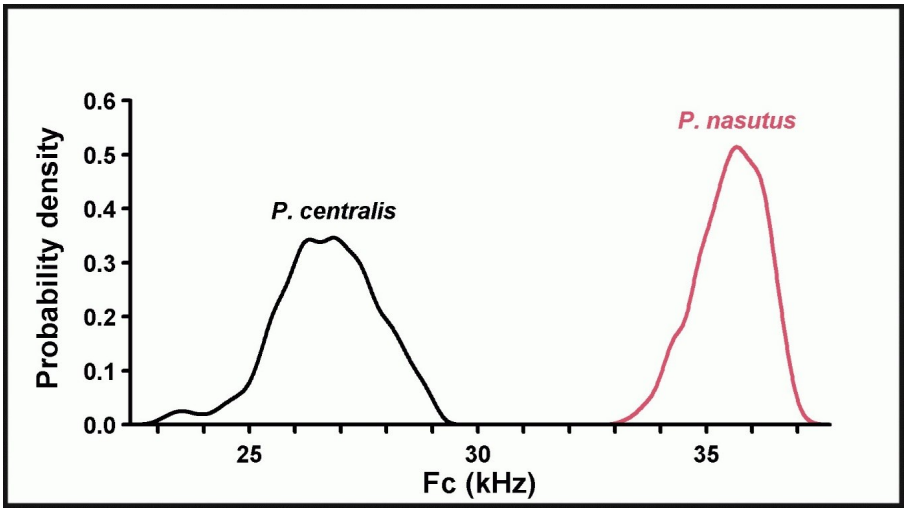

Fig. 3. Probability density plot of search phase of the dominant harmonic (Fc) for *Promops centralis* and *P. nasutus*. The average range includes both the increasing and decreasing FM pulses.

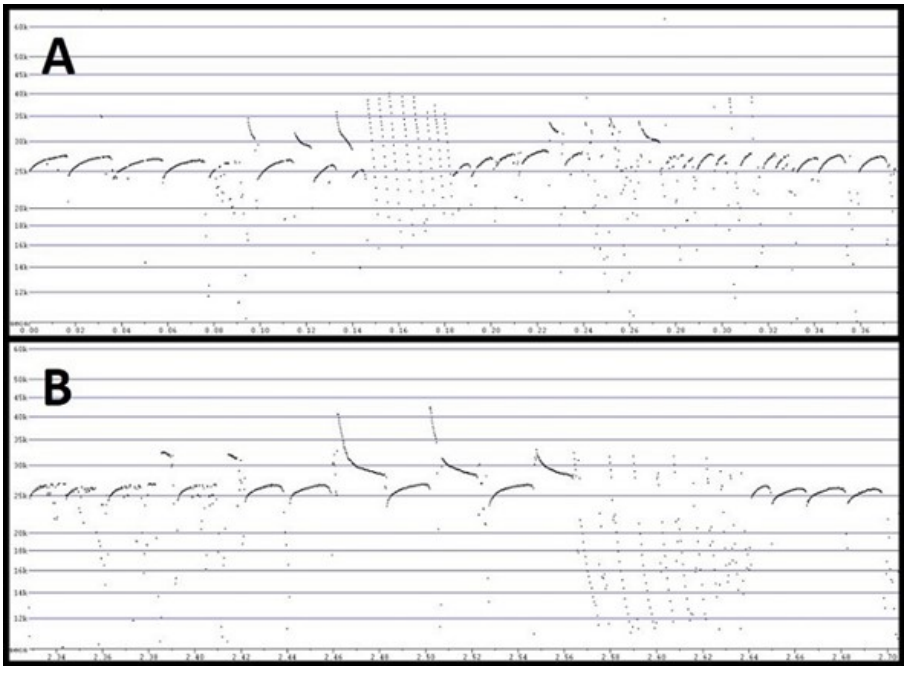

Fig. 4. Approach calls and feeding buzz of *P. centralis* from Venezuela, with the range spanning both the upper decreasing FM pulses and the lower increasing FM pulses (A), or mostly below both types of FM pulses (B).

erwise are seldom detected using capture methods alone (O'Farrell & Gannon 1999; Jung et al. 2014; MacSwiney-G et al. 2008). The advance of this type of studies in Venezuela, most of them focused on taxonomic inventories and ecological evaluations (Ochoa et al. 2000, 2005, 2009), has contributed to a better understanding of community assemblages, with a more robust estimate of the relative abundance of cryptic species previously considered rare or absent.

As is the case with other Neotropical aerial insectivorous bats that are poorly represented in collections and whose probabilities for detection increase with the use of acoustic methods (e.g., *Diclidurus* spp., *Centronycteris* spp., *Eumops* spp., and *Nyctinomops* spp.), the paucity of information across the entire geographic range of the genus *Promops* (Froidevaux et al. 2020; Hintze et al. 2020) represents an important historical limitation to understanding its role as a component of bat communities in many ecosystems. In this context, the new data presented here show that *P. centralis* and *P. nasutus* have considerably more extensive geographic and ecological distributions in Venezuela than suggested by previous reports (Linares 1998; Soriano et al. 2005; Ochoa et al. 2009). However, there is still a significant information gap for both species in the extreme northwest of the country, a large portion of the llanos, and several sectors of the region south of the Orinoco River.

Before this study, the distribution in Venezuela of *P. centralis* was thought to include the Andes of Mérida, the Central Coast Mountains Range, the Piedmont, Plains, and Low Hills of Guayana, and the Eastern Llanos (Handley 1976; Ochoa & Ibañez 1985; Linares 1998; Soriano et al. 2005; Eger 2008; Ochoa et al. 2009). Our results increase the knowledge on the occurrence of this bat to five additional bioregions and significantly extend its geographic distribution within the country. However, the presence of *P. centralis* in other regions of Venezuela could be expected if the spatial predictions proposed by Hintze et al. (2020) are considered, given the occurrence of this bat in a wide range of environmental conditions. This has been the case in Belize, where the species was unknown before acoustic samplings and is now recorded nearly across the entire country (Miller 2009). In Venezuela, *P. centralis* inhabits different ecosystems in a relatively wide altitudinal range, where the landscapes and the vegetation show different typologies (Huber 1997; Aguilera et al. 2003; Aymar 2011; Medina et al. 2013). This spectrum of ecological variations includes sectors where the current conditions are the result of modifications by the impacts associated with large-scale human activities (Bevilacqua et al. 2002; Rodríguez et al. 2010), as has been previously noted for this species (da Costa & Ramos Pereira 2022).

For *P. nasutus*, this study expands the known range to seven bioregions, including the first records for the Deltaic Plain of Delta Amacuro State, the Western Central Llanos of Guárico State, the Central Coast Mountain Range in Miranda State, and part of the Continental Coastal Strip (Sucre and Falcón States). While most of the records correspond to areas where continuous forests with a low level of disturbance represent the dominant vegetation, this bat was also recorded at a few locations with considerable habitat modifications where forest ecosystems are restricted to relict fragments associated with grasslands, crops, or urban developments. A recent evaluation of some ecological preferences of *P. nasutus* in Brazil, based on acoustic surveys (Sales & da Rocha 2024), reveals the relation of this species with synanthropic environments in areas where the landscape is a combination of fragmented forests and urban habitats. In fact, among a group of 15 non-phyllostomid species reported by these authors, only *P. nasutus* showed 100% of the acoustic records in urban conditions concerning forested sectors. However, Sales & da Rocha (2024) pointed out the rarity of *P. nasutus* in previous surveys conducted in Brazilian urbanized areas, where this bat has been occasionally found roosting in tree hollows and human structures.

The associations shown by *P. centralis* and *P. nasutus* to the presence of water bodies and open spaces in contact with forest edges, as borne out by the majority of our acoustic records, are consistent with the results described by other authors (Handley 1976; González-Terrazas et al. 2016; Yoh 2018; Froidevaux et al. 2020; Hintze et al. 2020). This apparent habitat association should be considered in sampling designs of future studies to increase the probability of documenting these species, as has been noted for other members of the family Molossidae (Ochoa 2000; Hintze et al. 2020). It is important to highlight that the use of acoustic methods in the study of Neotropical bats, in addition to providing information on echolocation patterns and the presence of species in a given area, is an effective tool to evaluate landscape relationships and ecological affinities (e.g., Jung & Kalko 2010; Bader et al. 2015; Yoh 2018; Hintze et al. 2020. These aspects represent valuable inputs to understanding habitat and population management needs and other conservation strategies (Sales & da Rocha 2024).

The apparent adaptability of some Neotropical aerial insectivorous bats to disturbed habitats or fragmented ecosystems has been suggested to be a favorable conservation attribute (Estrada-Villegas et al. 2010; Jung & Kalko 2011; Sales & da Rocha 2024); Therefore, given this tendency, *Promops* species may not be useful as indicators of the primary condition of some ecosystems (mainly forests), unlike other aerial insectivorous bats that are highly sensitive to

habitat modifications (Jung et al. 2007, 2014; Estrada-Villegas et al. 2010). Currently, *P. centralis* and *P. nasutus* are globally considered to be of Least Concern, according to the IUCN criteria (Solaris 2019; Bárquez & Díaz 2015) and have been excluded from the Red List of the Threatened Fauna in Venezuela (Rodríguez et al. 2015). Future studies will likely reveal more detailed information on the ecological preferences and distributional ranges of *Promops*, such as recently occurred with the first records of *P. davisoni* in Chile (Ossa et al. 2018) and *P. nasutus* for the state of Paraiba in Brazil (Sales & da Rocha 2024).

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ONLINE SUPPLEMENTARY MATERIAL

Appendix 1